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A NEW EARLY MIOCENE HERPETOFAUNA FROM KILÇAK, TURKEY

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The fauna of amphibians and reptiles (except turtles) from the early Miocene localities of the Kilçak section (Turkey) is described here. The herpetofaunal assemblage of the Kilçak localities is the best documented early Miocene herpetofauna in Anatolia. The following taxa are revealed: *Salamandra* sp., *Latonia* sp., *Eopelobates* sp., Crocodylia indet., Lacertidae indet. (morphotypes A and B), *Ophisaurus* sp., Anguinae indet., *Eoanilius* cf. *oligocenicus*, *Bavarioboa* sp., *Falseryx* sp., and *Texasophis* sp. Among them, *Latonia* represents the oldest published record of this frog in Anatolia. Its maxilla is sculptured, extending the occurrence of the *Latonia* lineage with ornamented maxillae to the earliest Miocene, and demonstrating the long coexistence of the *Latonia* lineages (with smooth and ornamented maxillae), for almost the entirety of the Late Cenozoic. The genera *Eopelobates*, *Eoanilius*, and *Falseryx* are described from Anatolia and Asia for the first time. The booid fauna, being poorly known from this time interval (i.e., the so called "Dark Period" of booid snakes), significantly adds to our knowledge of early Miocene snake assemblages. The snake material from Kilçak indicates a transition from "ancient" late Oligocene to "modern" early-middle Miocene fauna. The widely distributed European taxa recovered in Kilçak, indicate that Anatolia had close faunal links to Europe during the late Oligocene – early Miocene.

Keywords: herpetofauna; amphibians; reptiles; Miocene; Kilçak; Turkey.

INTRODUCTION

Anatolia has a very rich vertebrate fossil record from the Late Cenozoic due to the numerous terrestrial sedimentary basins that have accumulated vertebrate remains (e.g., Ünay et al., 2003). A large series of publications on the region primarily focused on small mammals (e.g., Ünay and de Bruijn, 1998), providing a regional biochronology, but the coeval herpetofauna of this area remain poorly documented. Most studies of amphibians and reptiles in Anatolia are based on material from the Plio-Pleistocene time interval, describing herpetofaunal assemblages from the Pliocene of Çalta (Rage and Sen, 1976), Çeştepe (Sen et al., 2017), and Ericek (Van den Hoek Ostende et al., 2015), the Early Pleistocene of Pasinler (Vasilyan et al., 2014), the Middle Pleistocene of Emirkaya-2 (Venczel and Sen, 1994), and the Pleistocene to early Holocene of Karain Cave (Zwick and Schleich, 1994). Fossil turtles are more well known from the Oligocene up to Quaternary (Malik and Nafiz, 1933; Paicheler et al., 1978; Tuna, 1988; Staesche et al., 2007), though their knowledge is still far more limited in comparison with adjacent areas (Georgalis and Kear, 2013). The current knowledge of the Miocene herpetofaunas are more problematic as data are very limited. The remains of some reptiles from several Turkish localities have been described in the last few years, including Oligocene and Miocene remains of anguids: *Ophisaurus*, *Anguis*, and indeterminate Anguidae (Čerňanský et al., 2017), and the

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Fig. 1. Schematic map of the localities.

Miocene remains of a blanid, *Blanus* cf. *strauchi* (Georgalis et al., 2018a). In addition, some herpetofaunal remains of the Miocene age are known from Bes Konak (also known as Beşkonak) and Alpagut-Dodurga localities, as well as from Mendikdere Formation in easternmost Turkey (Rückert-Ülkümen, 1980, 2003; Rückert-Ülkümen et al., 2002; Szyndlar and Hoşgör, 2012). A brief summary devoted to Miocene amphibians and the reptiles of Anatolia are reported by Claessens (1997).

Here we describe material of amphibians and reptiles from the Kilçak 0", Kilçak 0B, Kilçak 3A, and Kilçak 3B localities of the Kilçak section, which previously was known only in terms of mammalian fauna (Sickenberg et al., 1975; Van den Hoek Ostende, 1992, 1995a, 1995b; 1997, 2001a, 2001b, 2001c; De Bruijn and Saraç, 1992; de Bruijn et al., 1993, 2013; De Bruijn and Koenigswald, 1994; Ünay, 1994; Bosma et al., 2019). The micromammal assemblages of the Kilçak section enabled its correlation to MN 1 of the European continental scale, although Kilçak 0" and 0B are believed to represent the biostratigraphically oldest levels than Kilçak 3A and 3B (de Bruijn et al., 1993, 2013; de Bruijn and von Koenigswald, 1994; Sen et al., 1998). Previously, only anguid remains have been described from the herpetofaunal assemblage of the Kilçak section (Kilçak 3B locality; Čerňanský et al., 2017). New data allow us to reconstruct and discuss the taxonomic composition of the herpetofaunal assemblage of the Kilçak section. The herpetofauna from this age interval is rather rare and incompletely studied, but important for understanding climatic changes from the late Oligocene to the early Miocene, and transitions between Europe and Asia.

MATERIAL AND METHODS

The material is represented by isolated bones from the four localities of the Kilçak section: Kilçak 0", Kilçak 0B, Kilçak 3A, and Kilçak 3B (40°12′52.4″ N 33°24′20.5″ E; Fig. 1). The Kilçak section is situated in an open lignite quarry about 750 – 1000 m SE of Kilçak village, Alaplı District, Zonguldak Province, Turkey. The sediments of the Kilçak formation are lacustrine, mainly gray-green clay with several thin lignite horizons (Sen et al., 1998). The Kilçak formation is the oldest Neogene unit in the Çankýrý Basin (Central Anatolia). At present, the Kilçak section is completely covered by landslides (Kaymakçı, 2000).

An initial survey of the Kilçak region was conducted by one of the authors (G.S.) during the 1990s, and the area was later visited and sampled several times by EUNHM teams from 2000 to 2011. Eventually, the studied material was stored in the Natural History Museum of Ege University (EUNMH) in Izmir (Turkey). The described specimens were photographed using a scanning electron microscope (Tescan Vega-II XMU) in the Paleontological Institute of the Russian Academy of Sciences in Moscow (Russia) and the Leica M205 microscope and the Leica application suite V 3.3. 0 in the Department of Earth Sciences of the University of Torino (Italy). The osteological terminology for herpetofauna mainly follows Francis (1934), Roček (1984, 1994), Szyndlar (1984), and Sanchiz (1998).

SYSTEMATIC PALEONTOLOGY

Class Amphibia Gray, 1825
Order Caudata Fischer, 1813
Family Salamandridae Goldfuss, 1820
Genus *Salamandra* Laurenti, 1768
***Salamandra* sp.**
(Fig. 2)

Material. One trunk vertebra (EUNMH PV18000); Kilçak 3A locality.

Description. The centrum is opisthocoelous with relatively thick condyle indistinctly separated from the vertebral centrum. The length of the centrum is about 4.1 mm. The prezygapophyses are incomplete. The neural spine is long and low; it does not reach the posterior end of the neural arch. The neural arch is flattened. Its anteromedial notch is moderately developed. Posteriorly the neural arch is uplifted and has a medial notch. The rib-bearing processes are broken off near the bases on both sides, but it is clear from the remaining parts that they were double and cylindrical. In ventral view, two large and several small subcentral foramina are visible.

Remarks. The relatively small size of the centrum, together with a short neural spine that does not reach the posterior end of the neural arch, may suggest that the ver-

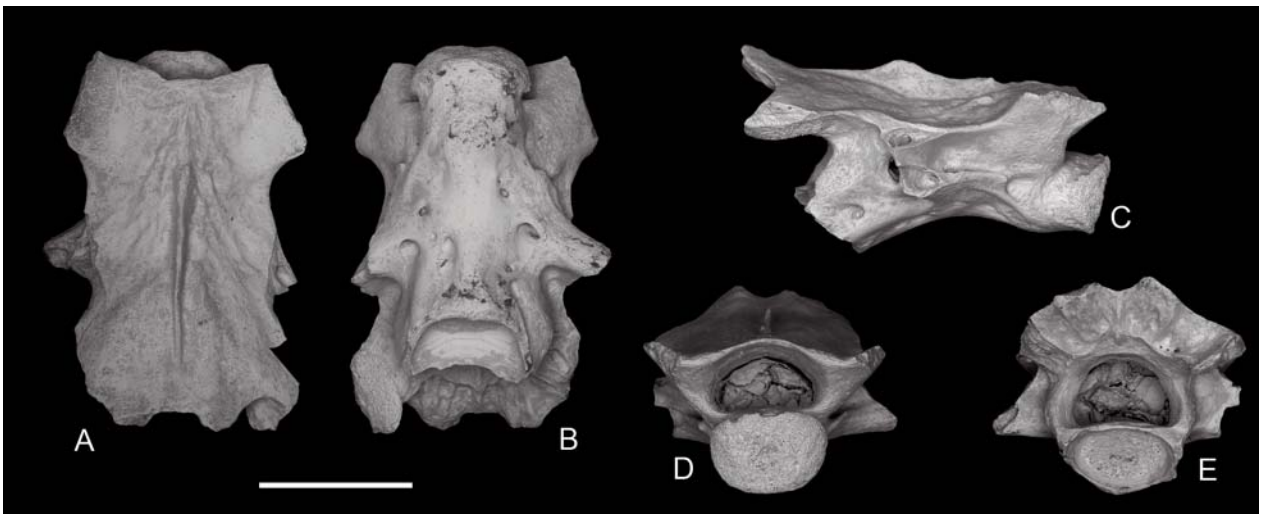

Fig. 2. *Salamandra* sp. from Kilçak 3A. A-E, trunk vertebra EUNMH PV18000, dorsal (A), ventral (B), lateral (C) view, anterior (D), and posterior (E) views. Scale equals 2 mm.

tebra from Kilçak belongs to *Salamandra salamandra*. However, another living species, *Salamandra infraimmaculata*, inhabits Turkey, Lebanon, Israel, and other Near East countries, however, it is so far unknown as fossils and its osteology is undescribed. Thus, to date *Salamandra* from Kilçak 3A cannot be determined with certainty to the species level.

Order Anura Fischer, 1813
Family Alytidae Fitzinger, 1843
Genus *Latonia* Meyer, 1843
***Latonia* sp.**
(Fig. 3A – L)

Material. One frontoparietal (EUNMH PV14100), two maxillae (EUNMH PV18004, 18005), Kilçak 0" locality; two maxillae (EUNMH PV18001, 18002), one centrum of V1 (EUNMH PV18003), Kilçak 3A locality.

Description. The frontoparietal (Fig. 3A, B) is represented by the posterior portion of the bone and shows the tubercular sculpture on its dorsal surface. Anteriorly, tubercles tend to merge into ridges. Sculpture does not reach the posterior margin of the dorsal surface. The base of the median crest is visible in the occipital lamella, which is preserved only by its anterior part. Ventrally, the posterior part of the frontoparietal incrassation and the posteriormost portion of the anterior part of the frontoparietal incrassation are preserved and not especially prominent above the level of the pars contacta. The contact facets for the prooticooccipitals are striated (as in all *Latonia*).

All maxillae (Fig. 3C – J) are incomplete and represented by the posterior parts of the bones. The sculptured area can be observed on the outer surface of both specimens from Kilçak 3A (Fig. 3C – F). In specimen EUNMH PV18001, it is located at the level of the processus zygomaticomaxillaris, whereas in specimen EUNMH PV 18002 it was seemingly wider and also covered the orbital part of the bone. The sculptured area consists of rugosity, but without clear tubercles or short ridges which are known in other *Latonia*. Two grooves running dorso-ventrally through the sculptured area are visible in specimen EUNMH PV18001. In lingual view, a broad horizontal lamina is visible. The tooth row exceed beyond the basis of the pterygoid process. The posterior depression on the inner surface of the bone (characteristic of *Latonia*) is clearly expressed in both specimens. It is delimited anteriorly by a ridge in specimen EUNMH PV18001. The maxillae from Kilçak 0" (Fig. 3G – J) are similar in size to maxillae from Kilçak 3A, but the formers lack a sculpture, i.e., the outer surface of the maxillae (including the basis of the processus zygomaticomaxillaris) is smooth. Only smooth wrinkles are observable along the orbital part of the bone. As for specimens from Kilçak 3A, in Kilçak 0" specimens the tooth row exceed beyond the basis of the pterygoid process and the posterior depression is visible, especially in specimen EUNMH PV18005.

The atlas (V1) from Kilçak 3A is incomplete; its neural arch is broken off (Fig. 3K). The centrum has a distinct median ridge on its ventral surface (Fig. 3L).

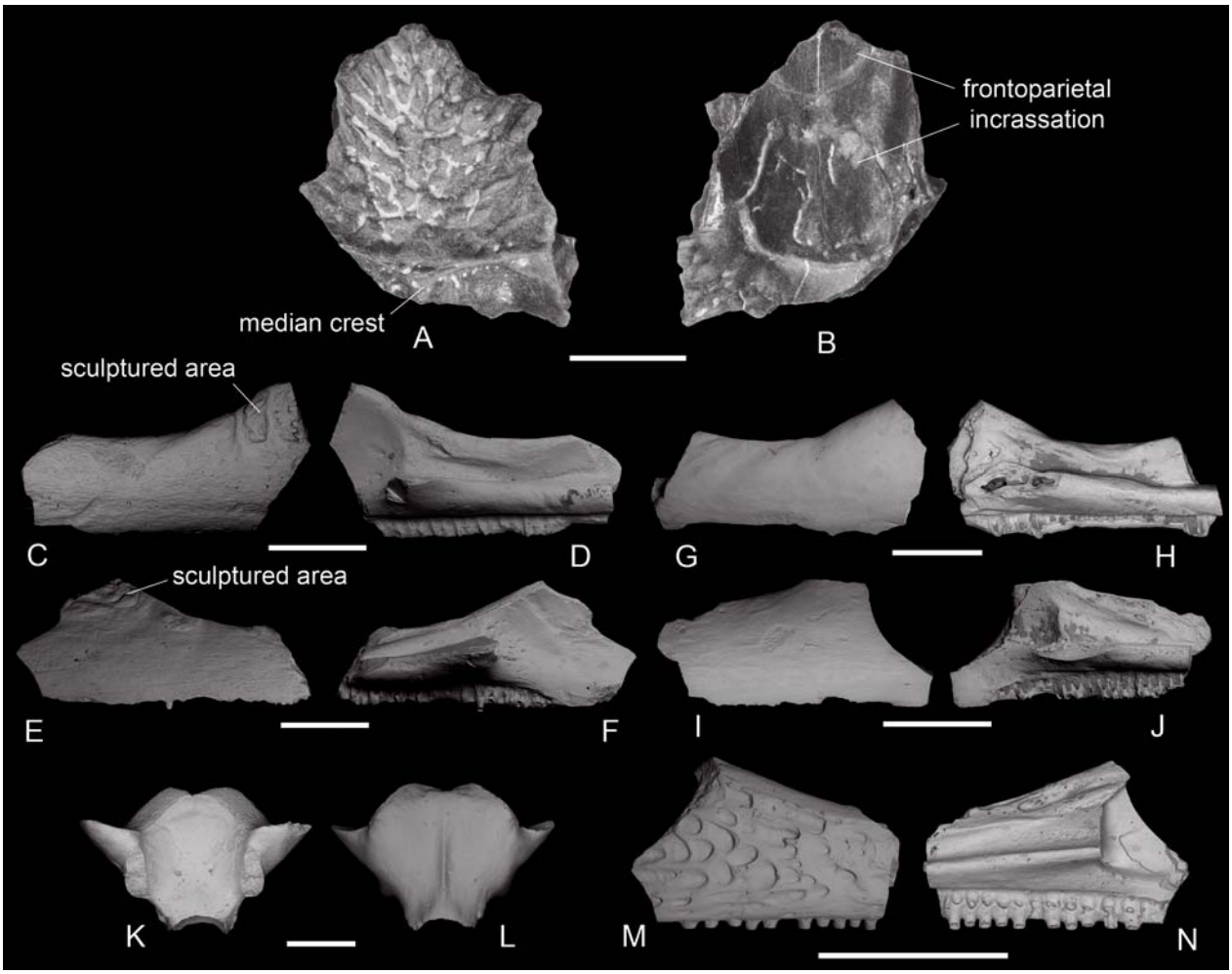

Fig. 3. *Latonia* sp. (A – L) and *Eopelobates* sp. (M-N) from Kilçak. A and B, frontoparietal of *Latonia* sp., EUNMH PV14100, Kilçak 0", dorsal (A), and ventral (B), views; C and D, left maxilla of *Latonia* sp., EUNMH PV18001, Kilçak 3A, labial (C) and lingual (D) views; E and F, right maxilla of *Latonia* sp., EUNMH PV18002, Kilçak 3A, labial (E) and lingual (F) views; G and H, left maxilla of *Latonia* sp., EUNMH PV18004, Kilçak 0", labial (G) and lingual (H) views; I and J, left maxilla of *Latonia* sp., EUNMH PV18005, Kilçak 0", labial (I) and lingual (J) views; K and L, atlas of *Latonia* sp., EUNMH PV18003, Kilçak 3A, dorsal (K) and ventral (L) views; M and N, right maxilla of *Eopelobates* sp., EUNMH PV18006, Kilçak 3A, labial (M) and lingual (N) views. Scales equal 2 mm.

Remarks. The absence of sculpturing of maxilla from Kilçak 0" can be explained by preservation reasons: the sculpture of *Latonia* is secondarily coalesced to the bone surface and may be crushed (see Roček, 1994). However, it may also indicate that maxillae from Kilçak 0" belong to the separate *Latonia* lineage (*Latonia* with smooth maxilla; see Syromyatnikova and Roček, 2018). Nevertheless, in other features (size and length of the tooth row), the maxillae from Kilçak 0" and Kilçak 3A are similar. Thus, here we provisionally assign all maxillae to a single taxon.

Latonia are among the most common fossil anurans in Europe, their earliest record being from the late Oligocene. During the late Oligocene-early Miocene the only *Latonia* with smooth maxillae (*Latonia ragei* and *L. vertaizoni*) is known (Roček, 1994). *Latonia* with sculptured maxillae made its first appearance in the early Miocene (MN 4) of Dolnice, Czech Republic (described as "*Miopelobates*" *fejfari*; Špinar, 1975; Hodrová, 1987) and Sant Mamet, Spain (Villa et al., 2017). Sculptured maxillae of *Latonia* have also been described from the early Miocene (MN 4) of Karydia (described as *Latonia* cf. *gigantea*) in Greece (Georgalis et al., 2019). *Latonia*

specimens from Kilçak 3A have a sculptured maxilla and extend the occurrence of *Latonia* with ornamented maxillae to the earliest Miocene (MN 1) (for recent data on *Latonia* distribution, see Syromyatnikova and Roček, 2018). From Turkey, *Latonia* (as *Latonia* sp.) was previously reported only from the Early Pleistocene of Pasinler (Vasilyan et al., 2014) and the Early Pliocene of Nasrettinhoca 2 (Syromyatnikova et al., personal observation). *Latonia* from Kilçak constitute the oldest published occurrence of this frog in Anatolia.

Family Pelobatidae Bonaparte, 1850
Genus *Eopelobates* Parker, 1929
***Eopelobates* sp.**
(Fig. 3M, N)

Material. One maxilla (EUNMH PV18006), Kilçak 3A locality.

Description. The maxilla is represented by the posterior portion of the bone. The labial surface of the maxilla is covered with sculpture consisting of rounded shallow pits bordered by smooth ridges (pit-and-ridge sculpture; sensu Roček et al., 2014). The pits are anteroposteriorly elongated, deep anteriorly rather than posteriorly, and may partially coalesce. In the lower part of the labial surface, the pits are more elongated and oval-shaped. In lingual view the robust and wide lamina horizontalis is visible. It markedly projects lingually. Posteriorly it terminates in a wide base of the pterygoid process (= processus pterygoideus). The tip of the pterygoid process is missing. The tooth row reaches the base of the pterygoid process and seemingly even extends behind it.

Remarks. The maxilla is assigned to *Eopelobates* based on the sculpture consisting of small and shallow pits. The pit-and-ridge sculpture is also characteristic of the Oligo-Miocene *Pelobates* clade (see Venczel, 2004), where it consists of well-marked pits and ridges, whereas in *Eopelobates* it consists of smooth and shallow pits and ridges.

Eopelobates is known in the Oligocene and Miocene of Europe (see Roček et al., 2014; Syromyatnikova, 2017). It is mostly known from Western and Central Europe. The *Eopelobates* fossil record is characterized by a stratigraphic gap between MP 30 and MN 4 (Roček et al., 2014), which may be filled now with the Kilçak 3A remains. The Kilçak 3A *Eopelobates* is the first published occurrence of the genus not only in Turkey but also from the entire Eastern Mediterranean. The only previously identified Asiatic record of *Eopelobates* sp. from the Zaisan Basin of Kazakhstan (Chkhikvadze, 1985) needs to be revised considering recent data on Pelobatidae.

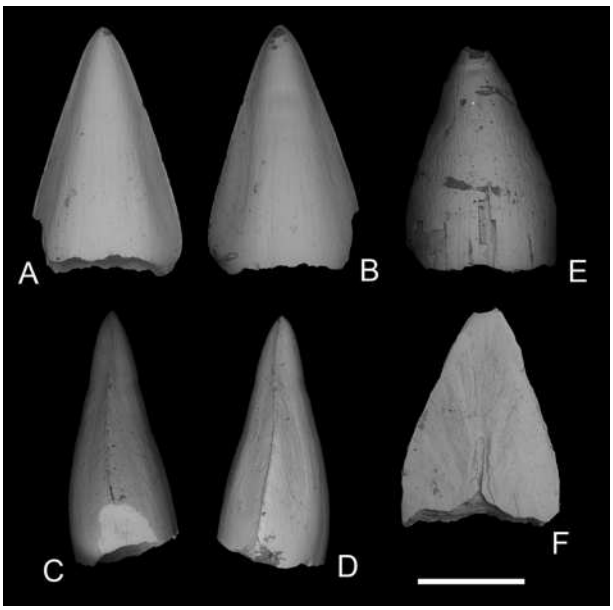

Fig. 4. Crocodylia indet. A-D: isolated tooth, EUNMH PV18008, Kilçak 3A, labial (A), lingual (B), and mesial (C, D) views; E, F, isolated tooth, EUNMH PV18007, Kilçak 0", labial (E) and lingual (F) views. Scale bar is 2 mm.

Class Reptilia Laurenti, 1768
Order Crocodylia Gmelin, 1789
Crocodylia indet.
(Fig. 4)

Material. Seven isolated teeth (EUNMH PV14093, 14108 – 14112, 18007), Kilçak 0" locality; two isolated teeth (EUNMH PV14119, 14120), Kilçak 0B locality; seven isolated teeth (EUNMH PV14127, 14136, 14138, 14140, 18008 – 18010), Kilçak 3A locality; three isolated teeth (EUNMH PV14143, 14158, 14165), Kilçak 3B locality.

Description. All isolated teeth are preserved only by crowns, which are conical. The teeth can be more or less massive. They are slightly curved lingually. Both surfaces are generally smooth with very small wrinkles and separated by unserrated mesiodistal carinae. The teeth from Kilçak 0" are relatively robust, with slightly wrinkled surfaces, but somewhat stronger than those from Kilçak 3A.

Remarks. The teeth of Crocodylia are not diagnostic a lower taxonomic level, precluding the precise identification of teeth from Kilçak. The crocodylian remains (mostly as isolated teeth) are widely known from Greek

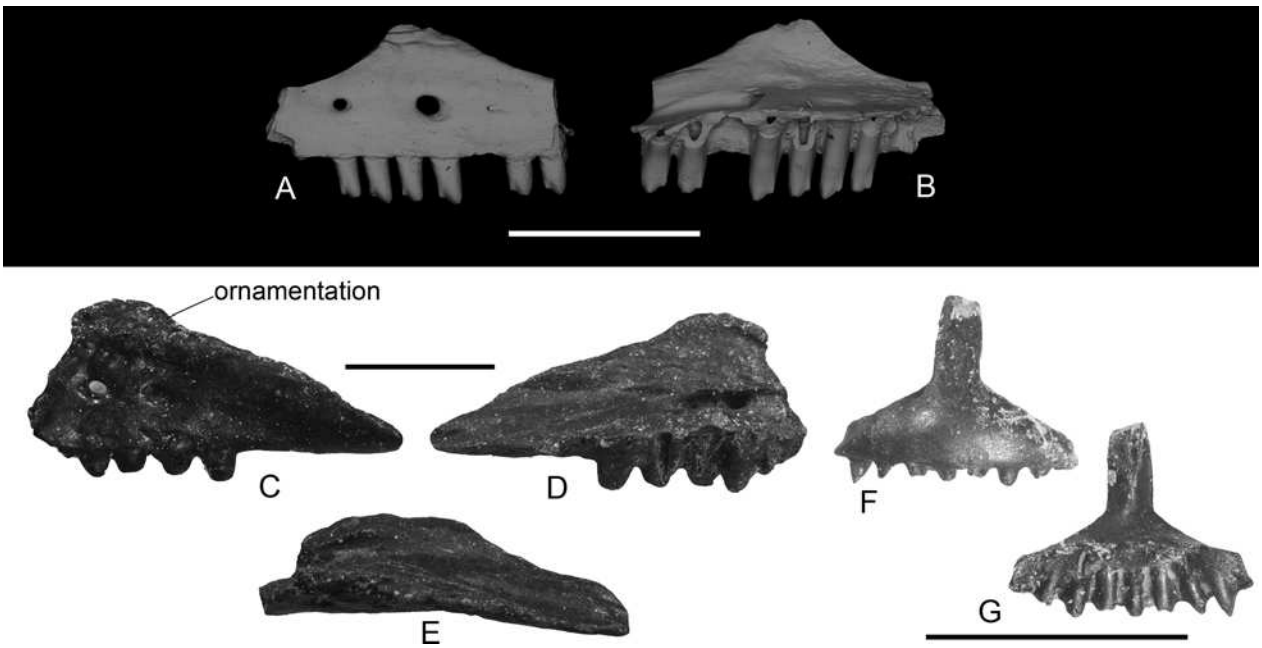

Fig. 5. Lacertidae from Kilçak. A and B, left maxilla of Lacertidae indet. (morphotype A), EUNMH PV18015, Kilçak 3A, labial (A) and lingual (B) views; C-E: left maxilla of Lacertidae indet. (morphotype B), EUNMH PV14094, Kilçak 0", labial (C), lingual (D), and dorsal (E) views; F and G, premaxilla of Lacertidae indet. (indeterminate morphotype), EUNMH PV 14157, Kilçak 3B, labial (F) and lingual (G) views. Scale bars are 2 mm.

localities of the early Miocene (Vasileiadou et al., 2017; Georgalis et al., 2019) and the late Miocene (Georgalis et al., 2016c). In contrast, Crocodylia from Turkey are poorly documented. They are known from the late Oligocene or early Miocene of Küçükdoğanca Köyü, in the European part of Turkey (Schelich, 1994) and by the single tooth of *Diplocynodon* (Alligatoroidea) from the early Miocene of Kağızman-Tuzluca Basin (Sen et al., 2011), and were mentioned from the early Miocene localities of Alahıdır (Salihli-Manisa) and Baloluk (Yahyalı-Kayseri) (Saraç, 2003). As was mentioned above, however, crocodylian teeth cannot be securely identified to the genus level, so accordingly, the attribution of the Kağızman-Tuzluca Basin tooth to the genus *Diplocynodon* should be taken only with much cautiousness.

Order Squamata Oppel, 1811
Family Lacertidae Oppel, 1811
Lacertidae indet. (morphotype A)
(Fig. 5A and B)

Material. Three dentaries (EUNMH PV14090, 14102, 14103), three maxillae (EUNMH PV14095, 14097, 14101), Kilçak 0" locality; two maxillae (EUNMH PV14134, 18015), Kilçak 3A locality.

Description. The maxilla EUNMH PV18015 (Fig. 5A and B) is represented by the middle part of the left element; the premaxillary and posterior processes are absent. The lateral surface of the bone bears three labial foramina. The foramina are significantly variable in size: the central foramen is very large, the anterior foramen is half the size of the central one, and the last foramen is minute. Only the base of the nasal process is preserved. The observed part of the nasal process is ornamented by smooth ridges and grooves. In medial view, a large alveolar foramen is visible, followed by a wide groove. The supradental shelf was seemingly expanded medially, although it is broken along the medial edge. All teeth are bicuspid, with a main cusp and an anteriorly placed small cusp. They become more robust posteriorly. The preserved portion of the maxilla bears eight tooth positions: six attached teeth and two tooth loci. Other maxillae and dentaries from Kilçak are fragmentary and represented by the middle part of the elements with bicuspid teeth.

Remarks. The maxillae and dentaries are assigned to Lacertidae based on tooth morphology. Lacertidae are abundant in modern-day Turkey as well as at the Pliocene (Çeştepe and Çalta; Rage and Sen, 1976; Sen et al., 2017) and Pleistocene (Emirkaya-2; Venczel and Sen, 1994) sites. In contrast, Miocene lacertids had not so far been

described from Anatolia. Therefore, the new remains described herein mark the first published record of lacertid lizards in the Miocene of the area. It should be noted that lacertids, even though only indeterminate records, are abundant in the early and late Miocene of Greece (Georgalis et al., 2017, 2019; Vasileiadou et al., 2017).

Lacertidae indet. (morphotype B)
(Fig. 5C – E)

Material. One left maxilla (EUNMH PV14094), Kilçak 0" locality.

Description. The maxilla is very poorly preserved with only the posterior portion of the bone preserved. The external surface has a small ornamented area dorsally to the labial foramina. Two foramina perforate the anterior part of the preserved portion of the bone. The observable portion of the maxilla bears six tooth positions with four teeth attached. In this area the supradental shelf is expanded medially. The area posterior to the last tooth position lacks dentition and bears a smooth groove dorsally. The teeth are robust, pleurodont, and cylindrical with blunt tooth crowns; cusps in the teeth are totally absent or only poorly distinguished.

Remarks. This maxilla seems to pertain to a distinct lacertid taxon than the above described specimens on the basis of its distinct, amblyodont dentition. Lacertids with amblyodont dentition were particularly common during the Paleogene of Europe (Müller, 2004; Augé, 2005), but they have also been described from the early Miocene of the central parts of the continent (Roček, 1984; Čerňanský et al., 2016a), and even known from the Pliocene of Balearics (Bailon et al., 2014). Overall, there seems to be a resemblance among the Anatolian specimen with *Janosikia ulmensis* (Gerhardt, 1903) from the early Miocene of Germany (see figures in Čerňanský et al., 2016a); nevertheless, more and better preserved material from Kilçak is needed before we can formally suggest any close or congeneric affinities between our new maxilla and *Janosikia*.

Lacertidae indet. (indeterminate morphotype)
(Fig. 5F, G)

Material. One premaxilla (EUNMH PV 14157) and a tooth bearing bone (EUNMH PV14149), Kilçak 3B locality.

Description and remarks. The premaxilla EUNMH PV 14157 is rather small. It bears eight tooth positions, with most teeth well preserved and several of which being almost complete. Its external surface is smooth. Teeth are rather slender and crowns of the left lateralmost one is almost acute and pointed. Premaxillae of lacertids cannot be confidently identified to the genus level. It is rather possible that this Kilçak premaxilla pertains to one of the above two described lacertid taxa. The same pertains to the isolated tooth bearing bone EUNMH PV14149.

Suborder Anguimorpha Fürbinger, 1900
Family Anguidae Gray, 1825
Subfamily Anguinae Gray, 1825
Genus *Ophisaurus* Daudin, 1803
***Ophisaurus* sp.**
(Fig. 6A – E)

Material. One trunk vertebra (EUNMH PV18011), Kilçak 3A locality.

Description. The trunk vertebra is incomplete and lacks its posterior part and anterior right prezygapophyses (Fig. 6A – E). The interzygapophyseal constriction is distinct. In ventral view, the lateral margins are slightly concave. The neural canal is high and nearly triangular in anterior and posterior views. Its height is slightly greater than that of the cotyle. The neural spine is incomplete, but it appears that it was relatively long (extending from the posterior edge of the prezygapophyses) and possibly inclined posteriorly. In dorsal view, the vertebra becomes wider posteriorly, having a triangular shape. The prezygapophyses are circular in shape and markedly laterally expanded. In anterior view, they are inclined from the horizontal plane at an angle of approximately 35°. Only the incomplete left postzygapophysis is observable. It is inclined from the horizontal plane at an angle of about 45°. The cotyle is dorsoventrally depressed and slightly slanting in lateral view.

Remarks. The trunk vertebra is assigned to *Ophisaurus* given that the height of the neural canal is slightly greater than that of the cotyle (Čerňanský et al., 2018). Fragmentary remains (fragment of the dentary and several trunk vertebrae) of *Ophisaurus* were recently described from several Oligo-Miocene Turkish localities (Kargi 2, Keseköy, Çandır C, Çandır HW, Bağiçi, and Süleymanli) (Čerňanský et al., 2017). *Ophisaurus* is also well known from several early and late Miocene localities from Greece (see Georgalis et al., 2017, 2019).

Anguinae indet.
(Fig. 6F – N)

Material. Two osteoderms (EUNMH PV14098, 14099), Kilçak 0" locality; one caudal vertebra (EUNMH PV18012), three osteoderms (EUNMH PV14130, 18013, 18014), Kilçak 3A locality.

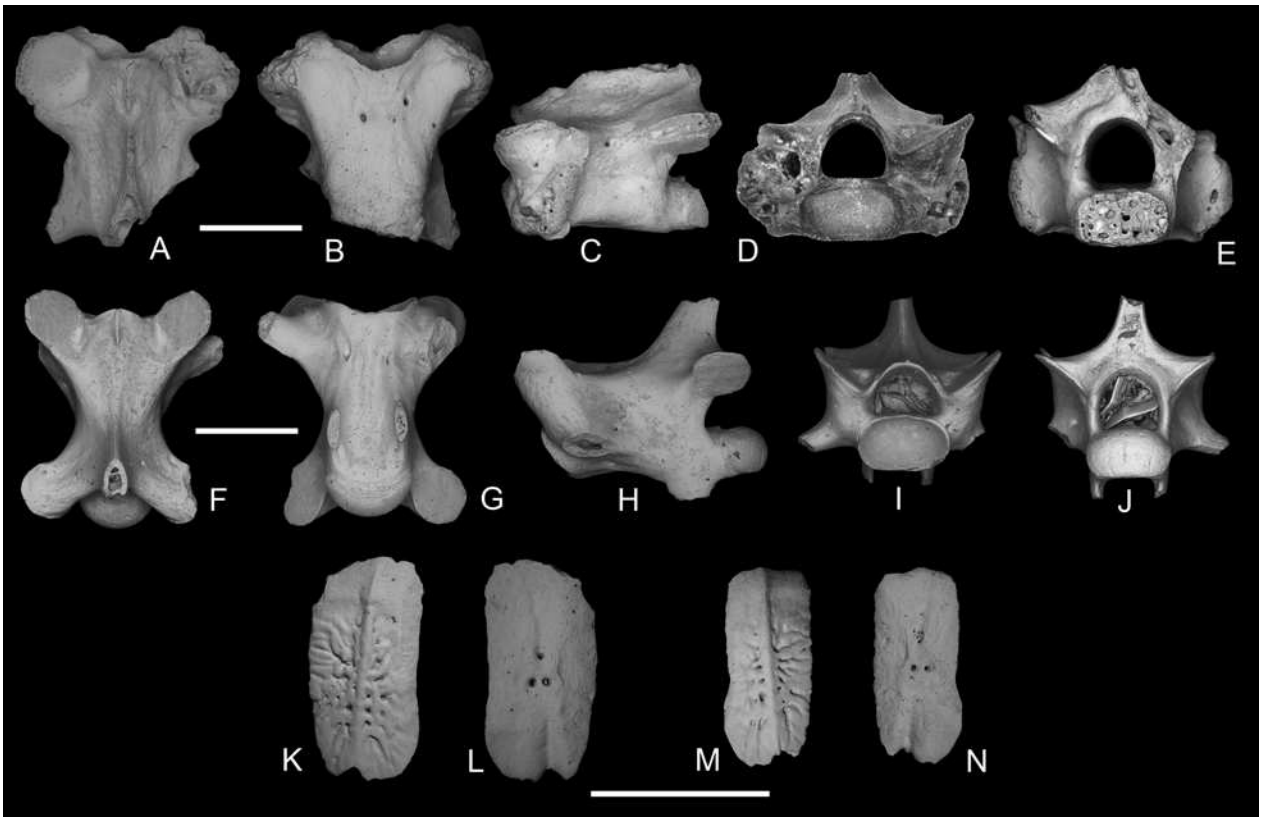

Fig. 6. Anguidae from Kilçak. A-E, trunk vertebra of *Ophisaurus* sp., EUNMH PV18011, Kilçak 3A, dorsal (A), ventral (B), lateral (C), anterior (D), and posterior (E) views; F – J: caudal vertebra of Anguinae indet., EUNMH PV18012, Kilçak 3A, dorsal (F), ventral (G), lateral (H), anterior (I), and posterior (J) views; K and L, osteoderm of Anguinae indet., EUNMH PV18013, Kilçak 3A, dorsal (K) and ventral (L) views; M and N, osteoderm of Anguinae indet., EUNMH PV18014, Kilçak 3A, dorsal (M) and ventral (N) views. Scale bars are 2 mm.

Description. The caudal vertebra (Fig. 6F – J) is narrow and anteroposteriorly elongated. The neural canal is wide and nearly triangular in anterior view, and highly arched in posterior view. The neural spine is confined only to the posterior region of the neural arch, where it is high and posteriorly inclined, although broken at its tip. The pre- and postzygapophyses are wide, bearing nearly circular articulation surfaces. They are inclined from the horizontal plane at an angle of about 50°. Both cotyle and condyle are dorsoventrally depressed. In lateral aspect, the cotyle is slanting, and the condyle protrudes well posteriorly. The bases of the haemapophyses are preserved on the ventral side on the centrum and fused to the bone. They are located closer to the condyle than to the cotyle. The only base of the transverse process is preserved solely on the right side of the vertebra.

The osteoderms (Fig. 6K – N) are small and slender, rectangular in shape, and with a low medial ridge running slightly obliquely along their central portions. The medial ridge continues on the gliding surface anteriorly to the ornamentation. The anterior overlap surface is smooth and occupies about one fifth of the external surface. The lateral bevel is poorly developed and narrow. The rest of the bone surface is covered by ornamentation, with low smooth grooves and small pits. The central part of the ventral surface in osteoderms is pierced by three foramina.

Remarks. The osteoderms EUNMH PV18013 and 18014 were found in the matrix embedded in the neural canal of the caudal vertebra. Affinities of the osteoderms with *Anguis* can be excluded, as in the latter genus these elements are non-rectangular (but they have an oval or irregular shape) and bear no keels. Therefore, it is possible that all osteoderms and the caudal vertebra belong to the *Ophisaurus*, as this is the sole known anguid genus from Kilçak. The described osteoderms are similar in size and morphology to those previously described from Kilçak 3B (Čerňanský et al., 2017: Fig. 4g).

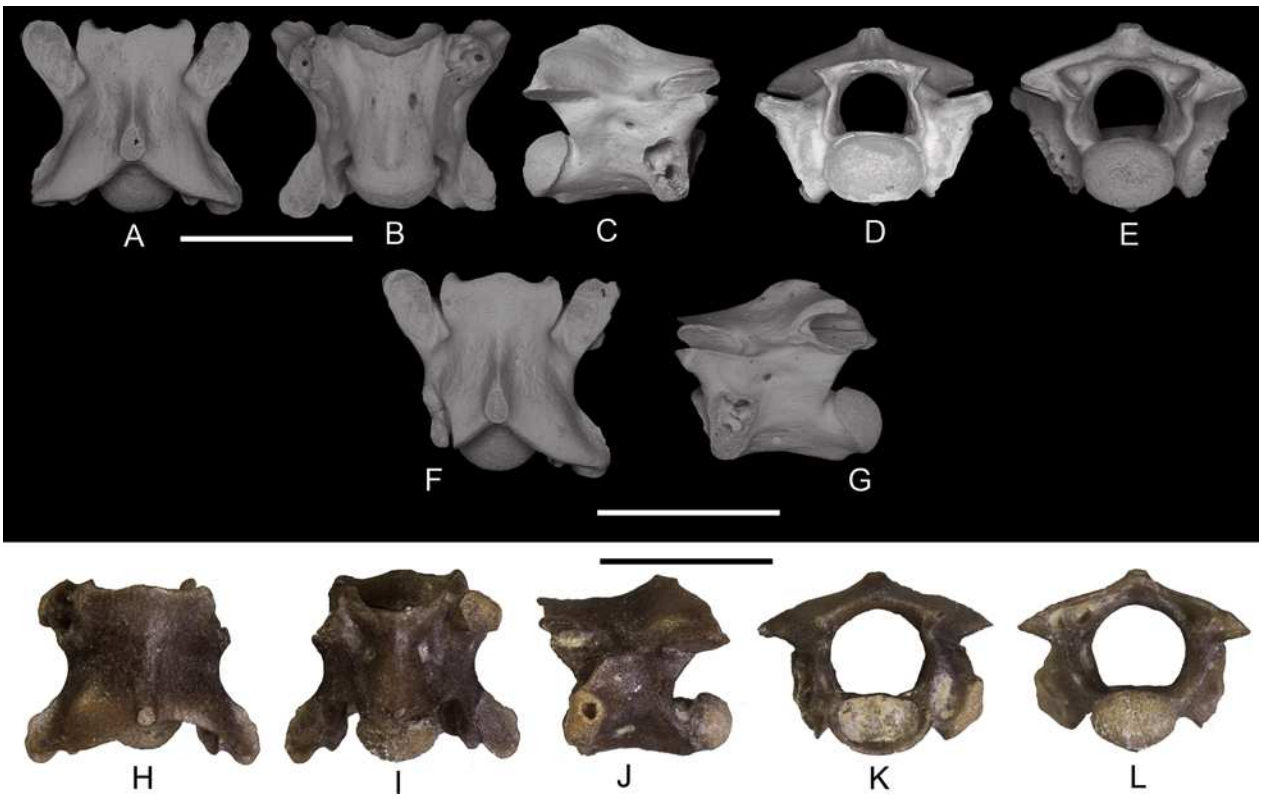

Fig. 7. *Eoanilius* cf. *oligocenicus* from Kilçak. A – E: trunk vertebra of *Eoanilius* cf. *oligocenicus*, EUNMH PV18016, Kilçak 3A, in dorsal (A), ventral (B), right lateral (C), anterior (D), and posterior (E) views; F and G: trunk vertebra of *Eoanilius* cf. *oligocenicus*, EUNMH PV18017, Kilçak 3A, in dorsal (F) and left lateral (G) views; H – L: trunk vertebra of *Eoanilius* cf. *oligocenicus*, EUNMH PV14154, Kilçak 3B, dorsal (H), ventral (I), left lateral (J), anterior (K), and posterior (L) views. Scales equal 2 mm.

Suborder Serpentes Linnaeus, 1758
Family Aniliidae Fitzinger, 1826
Genus *Eoanilius* Rage, 1974
***Eoanilius oligocenicus* Szyndlar, 1994**
***Eoanilius* cf. *oligocenicus* Szyndlar, 1994**
(Fig. 7)

Material. Three trunk vertebrae (EUNMH PV18016 – 18018), Kilçak 3A locality; two trunk vertebrae (EUNMH PV14154, 14159), Kilçak 3B locality.

Description. The vertebrae are small (the centrum length of the largest one being 1.5 mm). The centrum is about as wide as long. The haemal keel is shallow anteriorly and well-marked posteriorly; in the sole known posterior trunk vertebra (EUNMH PV 14159), the haemal keel becomes rather wide. The neural arch is depressed. The median notch of the posterior border of the neural arch is well marked. The neural spine is low and short, located far behind the zygosphene, and occupies about only one quarter of the neural arch length. The prezygapophyses are dorsally inclined in anterior view. The pre- and postzygapophyseal articular facets are oval-shaped and antero-posteriorly elongated. The prezygapophyseal processes are reduced and invisible in dorsal view. The zygosphenal roof is three-lobed with a wide central lobe in dorsal view. The cotyle and condyle are circular in shape. The paradiapophyses are incomplete in all specimens except the single parapophyseal process, which is preserved in the specimen EUNMH PV18017. The lateral and subcentral foramina are clearly visible. Paracotylar foramina are absent.

Remarks. The vertebrae are assigned to the genus *Eoanilius* based on their small size, the reduced neural spine located only at the posteriormost portion of the neural arch, the deep median notch in the posterior border of the neural arch, the dorsally inclined prezygapophyses, and the relatively shallow interzygapophyseal constriction (see characters in Rage, 1974). *Eoanilius* is an extinct genus that was present in Europe since the middle Eocene (MP 16 – 19, MP 20?; Rage, 2006) to the early middle Miocene (MN 5; Szyndlar, 2009; Čerňanský et

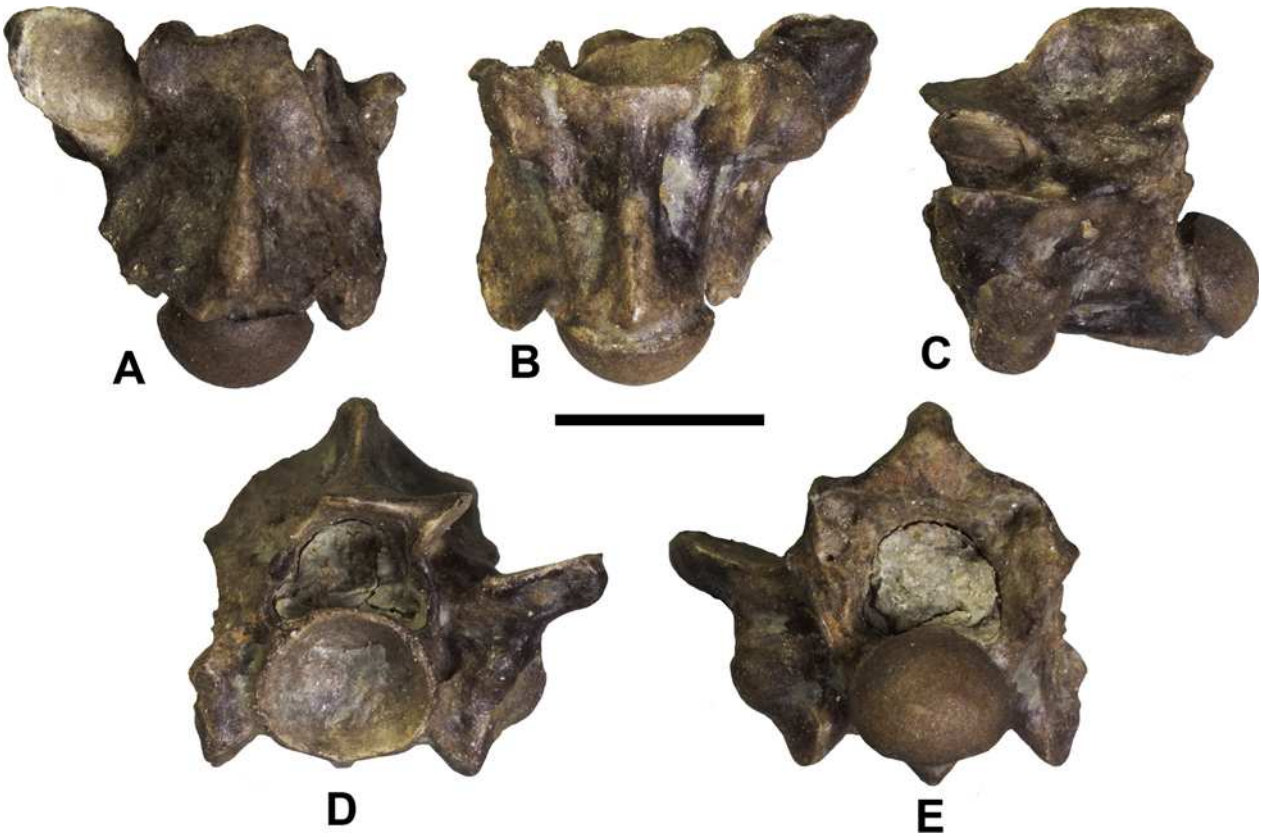

Fig. 8. *Bavarioboa* sp., EUNMH PV14147, Kilçak 3B, dorsal (A), ventral (B), left lateral (C), anterior (D), and posterior (E) views. Scale bar is 2 mm.

al., 2016b). The type species of the genus, *Eoanilius europae* Rage, 1974, is known only from the late Eocene of France (Rage 1974), whereas the younger taxon *Eoanilius oligocenicus* Szyndlar, 1994, has been reported from several German, French, and Italian localities dating from the early Oligocene (MP 22) to early Miocene (see Szyndlar, 1994, Szyndlar and Rage, 2003; Venczel and Sanchiz, 2006; Rage and Augé, 2015). During the early Miocene (MN 2 – 5), *Eoanilius* was widely present in Germany, where it even represented a dominant element in the middle-early Miocene (MN 2 and 3) snake assemblages (Szyndlar and Rage, 2003). *Eoanilius* from Kilçak closely resembles *Eoanilius oligocenicus* by having a well-defined haemal keel, a three-lobed zygosphene, and distinct subcentral and lateral foramina (see characters in Szyndlar, 1994). The currently known distribution of *Eoanilius* is restricted to Western European countries (Germany, France, Italy, and Spain). As such, the herein described material of *Eoanilius* from Kilçak expands its known distribution as far as Asia Minor.

It is worth noting that *Eoanilius* was originally placed in the family Aniliidae (whose recent distribution is confined to tropical America), however, recent authors have casted doubt on such affinities (Smith, 2013). Furthermore, current molecular data have suggested radically different topologies for aniliids, recovering most probable affinities with tropidophiids instead of the Asian cylindrophiids (e.g., Pyron et al., 2013) as it was traditionally considered on the basis of morphological evidence. These being said, any suggestion for close affinities of *Eoanilius* with extant aniliids should only be considered as tentative.

Superfamily Booidea Gray, 1825
Genus *Bavarioboa* Szyndlar et Schleich, 1993
***Bavarioboa* sp.**
(Fig. 8)

Material. One posterior trunk vertebra (EUNMH PV14129), Kilçak 3A locality; two posterior trunk vertebrae (EUNMH PV14147, 14162), Kilçak 3B locality.

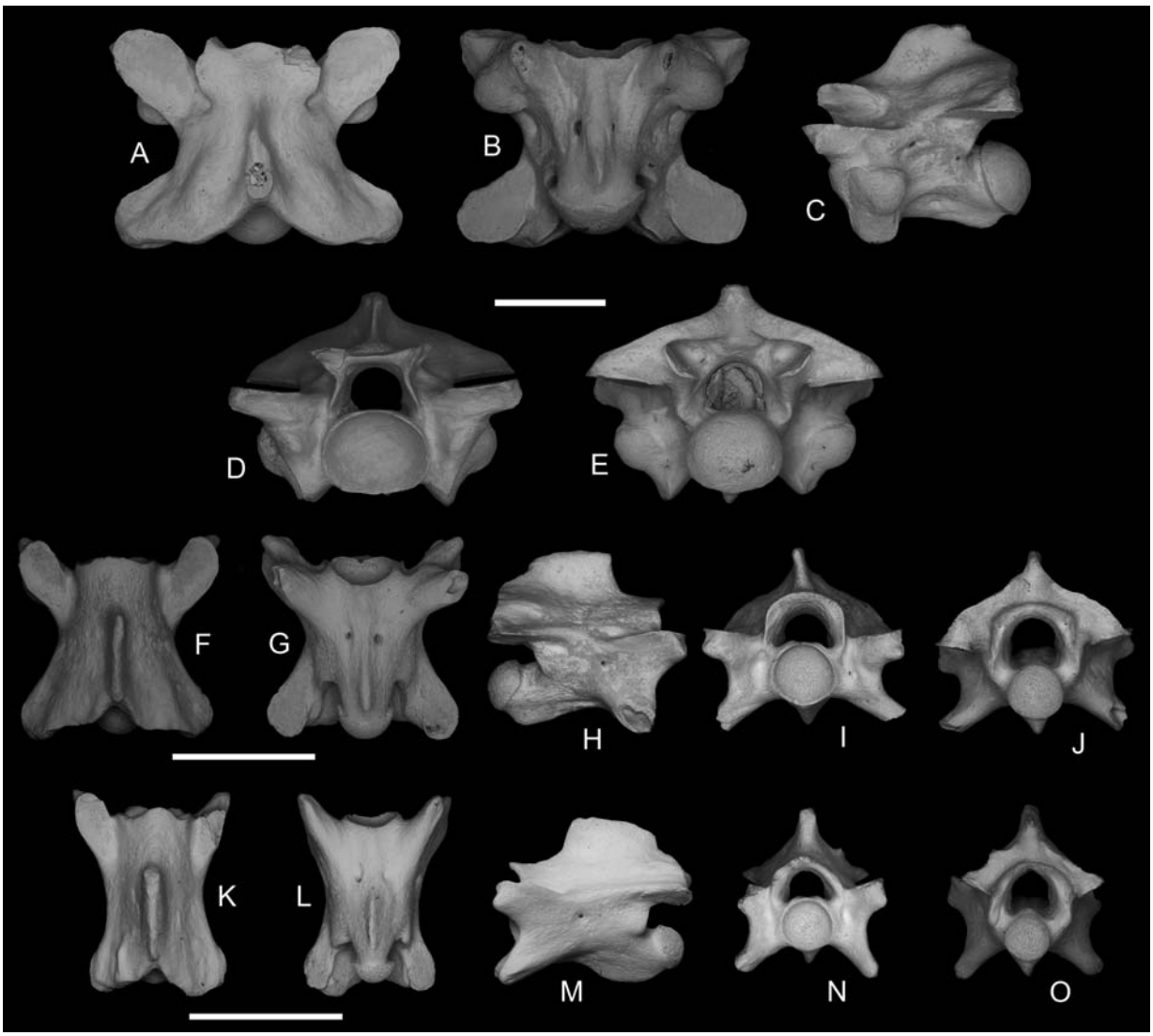

Fig. 9. *Falseryx* sp. from Kilçak 3A. A-E, trunk vertebra of *Falseryx* sp., EUNMH PV18019, dorsal (A), ventral (B), left lateral (C), anterior (D), and posterior (E) views; F-J, anterior caudal vertebra of *Falseryx* sp., EUNMH PV18077, dorsal (F), ventral (G), right lateral (H), anterior (I), and posterior (J) views; K-O, posterior caudal vertebra of *Falseryx* sp., EUNMH PV18078, dorsal (K), ventral (L), left lateral (M), anterior (N), and posterior (O) views. Scale bars are 2 mm.

Description. All vertebrae are incomplete. The largest vertebra has a centrum length of about 3.2 mm. In lateral view, the vertebra is slightly higher than long. The centrum is about as wide as long. The haemal keel is distinct and broad, uniform in width throughout its length. In lateral view, it has a straight ventral margin. The subcentral ridges are sharp and the subcentral grooves are relatively deep, features that along with the fact that the haemal keel is wide, indicate that these three vertebrae pertain to the posterior trunk region of the vertebral column. Both cotyle and condyle are robust; the cotyle is nearly sphaerical, whereas the condyle is slightly flattened dorsoventrally. The neural arch is incomplete in all vertebrae but it seems that it was moderately vaulted in posterior view. The neural spine is relatively long, occupying about one half the length of the neural arch, distinctly thickened in its posterodorsal part; its anterior and posterior margins are oblique. The paradiapophyses are non clearly divided into diapophyseal and parapophyseal portions; they are higher than long anteroposteriorly and they project downwards beyond the cotyle lip. The zygosphene is only moderately thick in anterior view. The

zygosphenal roof is nearly straight in anterior view and three-lobed in dorsal view. The prezygapophyses are located above the floor of the neural canal and are slightly dorsally inclined in anterior view. The prezygapophyseal accessory processes are weakly developed and only slightly visible in dorsal view. Lateral foramina are present below the level of the interzygapophyseal constriction. Subcentral foramina are present and large; paracotylar foramina are absent, with the exception of EUNMH PV14162, where a rather tiny paracotylar foramen is present on the right of the cotyle.

Remarks. These three vertebrae are assigned to *Bavarioboa* based on the wide centrum, the moderately thick zygosphene in anterior view, the dorsally inclined prezygapophyses located above the floor of the neural canal, the relatively short neural spine, and the occasional presence of paracotylar foramina (see characters in Szyndlar and Schleich, 1993 and Szyndlar and Rage, 2003). Previously, *Bavarioboa* was unknown in Europe from the latest Oligocene (MP 29 – 30) to the early Miocene (MN 1 – 2) time interval (Szyndlar and Rage, 2003). It reappeared in Europe only in MN 3 (Merkur-North locality, Czech Republic), where it is represented by a small form (Ivanov, 2002). *Bavarioboa* from Kilçak is also a relatively small snake, as it can be judged from its small vertebral centrum lengths that do not reach the 5 mm. The late Oligocene or early Miocene remains of this snake have also been described from eastern Turkey (Szyndlar and Hoşgör, 2012), being until now sole known occurrences of this genus in the area. In any case, the identification of *Bavarioboa* in Kilçak provides the first stratigraphically definite evidence of the presence of this snake genus in the earliest Miocene (MN 1) and furthermore confirms its more widespread distribution in Eastern Mediterranean. As for the exact affinities of *Bavarioboa*, although it was originally and often placed into Boidae and more precisely close to boines, on the basis of the frequent presence of paracotylar foramina, recent advances in the taxonomy of boas and pythons have prompted for a more reluctant systematic assignments of most fossil "booids" from the Cenozoic of Europe (see Georgalis and Scheyer, 2019).

Family Tropidophiidae Cope, 1894
Genus *Falseryx* Szyndlar et Rage, 2003
***Falseryx* sp.**
(Fig. 9)

Material. One caudal vertebra (EUNMH PV14121), Kilçak 0B locality; 60 trunk vertebrae (EUNMH PV14123, 14125, 18019 – 18076), one cloacal or anterior caudal vertebra (EUNMH PV14124), eight caudal vertebrae (EUNMH PV18077 – 18084), Kilçak 3A locality; two trunk vertebrae (EUNMH PV14145, 14148), two caudal vertebrae (EUNMH PV14150, 14152), Kilçak 3B locality.

Description. The vertebrae from the mid-trunk portion (Fig. 9A – E) are somewhat wider than long in dorsal and ventral views. The vertebrae are relatively moderately large, with the centrum length being 2.4 mm in the largest well-preserved vertebra. The interzygapophyseal constriction is well developed. The neural arch is strongly depressed. The posterior border of the neural arch is moderately notched. The dorsal border of the neural spine is horizontal and slightly thickened dorsally. The centrum is slightly longer than wide (ratio centrum length/neural arch width — 1.1). The haemal keel is broad anteriorly and become narrow posteriorly. In anterior view, the zygosphene is wide (wider than the cotyle) and slightly concave. In dorsal view it is three-lobed. The prezygapophyses are only weakly inclined and lie above the level of the floor of the neural canal. The prezygapophyseal accessory processes are acute and short (usually not seen in dorsal view). The paradiapophyses are massive, distinctly higher than long in lateral view, and only weakly divided into para- and diapophyseal portions. They project downward beyond the cotyle lip. The cotyle and condyle are sphaerical and slightly dorsoventrally compressed. Cotylar processes (sensu LaDuke, 1991) formed by the ventral part of the cotylar rim are absent. Paracotylar foramina are absent.

Two vertebrae pertain to the cloacal or anterior caudal region and other eight ones pertain to the anterior and posterior caudal regions. In contrast to the trunk vertebrae, the anterior caudal vertebrae (Fig. 9F – J) have a longer centrum (which is longer than wide, ratio CL/NAW — 1.4) and longer neural spine (occupying more than half the neural arch length). The neural arch is somewhat vaulted and especially in the caudal vertebra EUNMH PV14150 it is exceptionally vaulted forming an acute triangle. The posterior border of the neural arch is notched in dorsal view. In contrast to the trunk vertebrae, neural spine is higher and and not thickened along the dorsal edge. The pleurapophyses are directed laterally. The centrum bears a short and distally pointed hypapophysis instead of haemapophyses. The zygosphene is narrow in dorsal view, and convex in anterior view. As in the case of trunk vertebrae, the prezygapophyseal accessory processes are acute and short, but they are visible in dorsal view. The cotyle and condyle are sphaerical and not depressed. Paracotylar foramina can be either present or absent, and only one foramen can be present (e.g., only the left foramen is visible, Fig. 9I). The posterior caudal

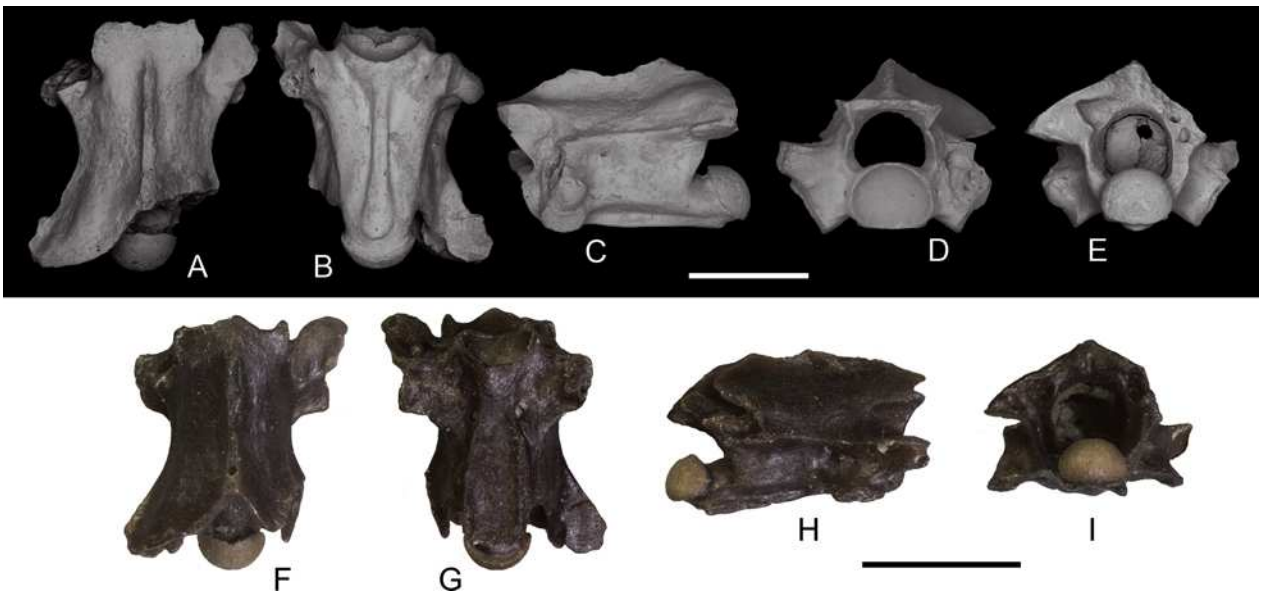

Fig. 10. *Texasophis* sp. from Kilçak. A-E, trunk vertebra, EUNMH PV18085, Kilçak 3A, dorsal (A), ventral (B), left lateral (C), anterior (D), and posterior (E) views; F-I, caudal vertebra, EUNMH PV14151, Kilçak 3B, dorsal (F), ventral (G), right lateral (H), and posterior (I) views. Scales equal 2 mm.

vertebrae (Fig. 9K – O) bear long and narrow centra (ratio CL/NAW — 1.7). In contrast to anterior caudal vertebrae, their pleurapophyses are directed antero-laterally. Ventrally, the short but ventrally prominent haemal keel is visible. Middle caudal vertebrae (which bear haemapophyses) are unknown.

Remarks. The vertebrae described here differ from *Bavarioboa* by having smaller size, a well-expressed interzygapophyseal constriction, a depressed neural arches, and neural spine restricted to the posterior portion of the neural arch in dorsal view; in these respects, these trunk vertebrae are most similar to *Bransateryx* and *Falseryx*. *Bransateryx* is a typical Erycinae in having shortened posterior caudal vertebrae with additional processes. The ophidian material from Kilçak includes more than 60 booid vertebrae from different portions of the vertebral column, but does not contain any erycine caudals. It also differs from *Rottophis* and *Platyspondylia* by having larger and more heavily built trunk vertebrae and distinct prezygapophyseal processes. We thus, refer this material from Kilçak to *Falseryx*, with which it also shares strongly resemblance in terms of its depressed neural arches, and neural spine restricted to the posterior portion of the neural arch in dorsal view (Szyndlar and Rage, 2003).

Falseryx has so far been described from MP 21 (early Oligocene) of Belgium (*Falseryx neervelpensis*; Szyndlar et al., 2008) and MN 4 (early Miocene) of Germany and the Czech Republic (the type species, *Falseryx petersbuchi*; Szyndlar and Rage, 2003). This genus may also be present in MN 2 (early Miocene) of Germany (Čerňanský et al., 2015), MN 3 or 4 in Spain and MN 5 and MN 7+8 (middle Miocene) of Germany (Szyndlar and Rage, 2003; Čerňanský et al., 2016b). The described vertebrae from Kilçak clearly differ from *Falseryx neervelpensis* in their shorter centra, stronger interzygapophyseal constriction, higher and more dorsally thin neural spine, presence of central lobe of zygosphene, and larger and more dorsoventrally extended paradiapophyses. At the same time, they closely resemble the geologically younger *Falseryx petersbuchi*, although they differ somewhat in terms of prezygapophyseal processes and posteriorly narrower haemal keel. *Falseryx* from Kilçak represents the first Anatolian record of this genus and fills a temporal gap in the record of *Falseryx* between MP 22 and MN 2 or 3 (see Čerňanský et al., 2015), while it provides a significant expansion in its geographic distribution.

Family Colubridae Oppel, 1811
Genus *Texasophis* Holman, 1977
***Texasophis* sp.**
(Fig. 10)

Material. One trunk vertebra (EUNMH PV14115), Kilçak 0" locality; three trunk vertebrae (EUNMH PV14133, 18085 – 18087), Kilçak 3A locality; one trunk vertebra (EUNMH PV14146), one caudal vertebra (EUNMH PV14151), Kilçak 3B locality.

Description. All trunk vertebrae are incomplete (Fig. 10A – E). The centrum is elongated (its length reaches 4 mm). The neural arch is moderately vaulted. The dorsal margin of the neural spine is broken off, but was seemingly long and low. The haemal keel is well defined, widened posteriorly and flattened ventrally. It is clear visible also in lateral view. The subcentral surface is flat or bears clear subcentral grooves. The subcentral ridges are sharp. Cotyles and condyles are nearly circular. Synapophyses are divided into diapophyses and parapophyses; the diapophyses are rounded in shape, while the parapophyses are slightly elongated anteroposteriorly (longer than diapophyses). They are separated by a shallow depression. Although incomplete, the zygosphene was obviously three-lobed in dorsal view. It is relatively thin in anterior view, with its zygosphenal roof being nearly straight.

The single caudal vertebra probably comes from the anterior caudal region (Fig. 10F – I). Ventrally, it bears paired haemapophyses. They are well-developed and directed ventrolaterally. Apart from these features, the length and morphology of the vertebra is generally reminiscent of that observed in the trunk vertebra. In contrast to trunk vertebra, the cotyles and condyles are relatively compressed dorsoventrally. The zygosphene is three-lobed in dorsal view with strongly developed central lobe.

Remarks. All vertebrae are incomplete, but they bear strong resemblance to *Texasophis* in having an elongate centrum, a long and low neural spine, a moderately vaulted neural arch, and a prominent haemal keel (Holman, 1977; Rage, 1984). *Texasophis* was originally established from North America (Holman, 1977), but several subsequent finds have been referred to this genus from the Oligocene to the middle Miocene of both North America and Europe (Rage and Holman, 1984; Szyndlar, 1991; Holman, 2000), confirming thus a rather wide geographic and stratigraphic distribution. Within the European congeners, *Texasophis* from Kilçak differs from *Texasophis meini* Rage et Holman, 1984 from La-Grive-Saint-Alban (MN 7+8, France) by its narrow haemal keel (Rage and Holman, 1984), from *Texasophis hecki* Böhme, 2008 from Oberleichtersbach (MP 30, Germany) by its shallow subcentral grooves, while it bears similarity to both the latter species and *Texasophis bohemiacus* Szyndlar, 1987 from Dolnice (MN 4, Czech Republic) in having a three-lobed zygosphene (Szyndlar, 1987).

Caudal vertebrae of *Texasophis* have been so far known for *Texasophis bohemiacus* Szyndlar, 1987 (Szyndlar, 1994), where only the single vertebra from the posterior caudal region was figured. The caudal vertebra from Kilçak pertains to the anterior caudal region. Similarly to that of *T. bohemiacus*, it has a relatively well-developed central lobe of the zygosphene.

DISCUSSION

The fossil herpetofauna of Kilçak section is mainly composed of taxa that are absent in modern-day Anatolia (*Latonia*, *Ophisaurus*, and Crocodylia) or are totally extinct (*Eopelobates*, *Eoanilius* cf. *oligocenicus*, *Bavarioboa*, and *Falseryx*). Among them, *Latonia* represent the oldest occurrence of this frog in Anatolia; *Eopelobates*, *Eoanilius*, and *Falseryx* were previously unknown in Anatolia and Asia, which would now shows an important part of their biogeographic history and distribution.

Latonia from Kilçak greatly contributes to our comprehension of the distribution of the genus. It shows the sculptured maxillae (Fig. 3C – F). This character, the most important for *Latonia* systematics (Roček, 1994), is observed in the genus at the beginning of the MN 4 (Dolnice and Sant Mamet localities). In contrast, in the oldest known *Latonia* (*L. vertaizoni* from upper Oligocene of the Coderet, MP 30, France) the maxilla is smooth (*Latonia* lineage with smooth maxillae; see Syromyatnikova and Roček, 2018). *Latonia* from Kilçak constitutes the first sculptured *Latonia* from MN 1. This record, therefore, extends the *Latonia* lineage with ornamented maxillae to the earliest Miocene, and shows the long coexistence of both *Latonia* lineages during almost the whole Late Cenozoic.

The most numerous fossils in Kilçak are snakes: *Eoanilius* cf. *oligocenicus*, *Falseryx* sp., *Bavarioboa*, and *Texasophis* sp., which all pertain to relatively small-sized forms. Especially for *Eoanilius* and the "booids" *Falseryx* and *Bavarioboa*, they occur in the earliest Miocene of Anatolia as elements of "ancient" late Oligocene faunas. This is not surprising, given that small "booids" are typical for European fauna of the latest Oligocene (MP 29 – 30) to earliest Miocene (MN 1 – 2). This period is called the "Dark Period" for booid snakes, when the diversity of "booids" strongly decreased (Rage and

Szyndlar, 2005). During the Dark Period, several "booids" were identified in Europe: booid *Bavarioboa*, erycine *Bransateryx* and tropidophiids *Falseryx*, *Platyspondylia*, and *Rottophis*. Among them, *Bransateryx* is the most common booid for the Dark Period. However, *Bransateryx* is absent in Kilçak fauna. The most common "booid" in Kilçak is *Falseryx* that is unusual for this time interval. Seemingly, it becomes a dominant element in Kilçak 3a. During that time it was only present in Amöneburg (Čerňanský et al., 2015). *Bavarioboa*, is a relatively large-sized snake, though it is represented in Kilçak by a small form. But this should not appear at strange as small-sized *Bavarioboa* has also been described from the early Miocene (MN 3) of Merkur-North (Ivanov, 2002).

Eoanilius, *Falseryx*, and *Bavarioboa* co-occurred together in Kilçak, a pattern that is similar to certain European localities (Szyndlar and Rage, 2003). The presence of both *Falseryx* and *Eoanilius* is known from the earliest Oligocene (MP 21) of Boutersem-TGV (Szyndlar et al., 2008), early Miocene (MN 3 – 4) of Agramón (Szyndlar and Alférez, 2005), and early Miocene (MN 4) of Petersbuch 2 (Szyndlar and Rage, 2003). *Eoanilius* and *Bavarioboa* co-occurred in the late Oligocene (MP 28 – 30) of Herrlingen 8 and 11; *Bavarioboa* and *Falseryx* co-occurred in the early Miocene (MN 4) of Dolnice (Szyndlar and Rage, 2003). All these three taxa (*Eoanilius*, *Falseryx*, and *Bavarioboa*) are found together only in the early Miocene (MN 4) of Petersbuch 2 (Szyndlar and Schleich, 1993) and the middle Miocene (MN 5) of Hambach (Čerňanský et al., 2016b).

No record of *Falseryx* is known between MP 22 and MN 2 or 3 (Čerňanský et al., 2015). Thus, *Falseryx* from Kilçak fills this temporal gap in the record of this genus. The situation is similar to *Bavarioboa*, which is unknown in Europe from the latest Oligocene (MP 29 – 30) to earliest Miocene (MN 1 – 2) time interval and reappeared only in MN 3.

Other snake material from Kilçak indicates a change from "ancient" to "modern" early-middle Miocene faunas. Colubridae are among the newcomers. Although they were present in Europe since the beginning of the Oligocene, they started to dominate only after MN 2 and gradually displaced the representatives of "booids" (Ivanov, 2001; Szyndlar, 2012). *Texasophis*, indicating "modern" faunal snake, is probably oriental immigrant (Szyndlar, 1994) and had two dispersals to Europe. Second visit of *Texasophis* was in the late early Miocene (MN 4) (Szyndlar, 1987). *Texasophis* from Kilçak, possibly, survived from the Oligocene lineage of the genus. Interestingly, besides *Texasophis*, there are no other colubrid taxa known from Kilçak; colubrids consist the dominant snake group in Europe today, having a rich Miocene record in nearby areas of Anatolia, such as Greece (Georgalis et al., 2017, 2018b). As far as it regards other "modern" snakes (i.e., caenophidians), remains of vipers and/or cobras were not found in Kilçak, although the former have been recorded in Europe since the earliest Miocene (MN 1) (Szyndlar and Schleich, 1993; Szyndlar and Rage, 2002), while cobras appear slightly later (Szyndlar and Rage, 1990; Kuch et al., 2006). Cobras have their first record in Anatolia during the Pliocene (Rage and Sen, 1976), whereas both vipers and cobras are known from older sediments in nearby Greece (Georgalis et al., 2016a, 2018b, 2019).

The Kilçak material displays a moderate diversity herpetofaunal assemblage including of 12 taxa of amphibians and reptiles which cannot be definitively assigned to the species level. The herpetofauna of all Kilçak localities displays a generally homogeneous compo-

TABLE 1. Faunal list of Kilçak sections. Anguidae indet. from Kilçak 3B listed according to Čerňanský et al. (2017).

		Kilçak 0"	Kilçak 0B	Kilçak 3A	Kilçak 3B
Amphibia	Salamandridae	—	—	*Salamandra* sp.	—
	Alytidae	*Latonia* sp.	—	*Latonia* sp.	—
	Pelobatidae	—	—	*Eopelobates* sp.	—
Reptilia	Crocodylia	Crocodylia indet.	Crocodylia indet.	Crocodylia indet.	Crocodylia indet.
	Anguidae	—	—	*Ophisaurus* sp.	—
		Anguinae indet.	—	Anguinae indet.	Anguidae indet.
	Lacertidae	Lacertidae indet. (morphotypes A and B)	—	Lacertidae indet. (morphotype A)	Lacertidae indet. (morphotype indet.)
	Aniliidae	—	—	*Eoanilius* cf. *oligocenicus*	*Eoanilius* cf. *oligocenicus*
	Booidea	—	—	*Bavarioboa* sp.	*Bavarioboa* sp.
	Tropidophiidae	—	*Falseryx* sp.	*Falseryx* sp.	*Falseryx* sp.
	Colubridae	*Texasophis* sp.	—	*Texasophis* sp.	*Texasophis* sp.

sition of elements (Table 1). It is mostly dominated by squamates, whereas amphibians are diverse only in Kilçak 3A. Most of squamates occur in all Kilçak localities except Kilçak 0B. But such faunistic differences might be explained by the fact that Kilçak 0B yielded lower amount of fossils. In terms of taxonomic richness, the Kilçak herpetofauna approached with the Turkish Plio-Pleistocene localities of Çalta (12 taxa) and Emirkaya-2 (11 taxa). However, the faunal composition from the Miocene of Kilçak differs from those of Çalta and Emirkaya-2: they both share only two taxa with Kilçak. Comparison with the Miocene Turkish localities is difficult due to incomplete data on their fauna. Nevertheless, Kilçak notably lacks any amphisbaenian remains, unlike the locality of Gebeceler (MN 7+8), which has yielded the so far earliest occurrence of *Blanus* in Anatolia, a genus that still exists in the extant herpetofauna of the region (Georgalis et al., 2018a). The Kilçak herpetofauna is generally more similar to the early Miocene faunas of Europe. The earliest Miocene faunas from Europe are poorly known due to the scarcity of localities of this age and are usually neither rich nor diverse. The localities of MN 1 and MN 2 are mostly known from Germany and France. The most well-known fauna of MN 2 (Amöneburg) is more diverse than Kilçak, and includes *Pseudopus*, *Ophisaurus*, two small booids (?*Falseryx* and booid indet.), and several Colubridae. The trunk vertebra of *Ophisaurus* from Kilçak is very similar to those from Amöneburg (Čerňanský et al., 2015: Fig. 9C, D). Other taxa occurring in the Amöneburg (i.e., Shinisauria, Scincomorpha, Blanidae, Gekkota, Natricinae, Viperidae) are, however, absent among the Kilçak collection. Unfortunately, amphibian fauna of Amöneburg is so far unknown. Also, in contrast to Kilçak, the slightly older fauna of MP 30 (Oberleichtersbach) is more diverse; however, it shares with Kilçak the presence of *Eoanilius* and *Texasophis*. In the Mediterranean area, the oldest known Greek herpetofaunas are known from the MN 3 zone of Lapsarna, Lesbos Island (Vasileiadou et al., 2017) and Kymi, Euboea Island (Römer, 1870) localities, while slightly younger (MN 4) herpetofaunas are better documented, i.e., Aliveri (also in Euboea Island) and Karydia (Georgalis et al., 2016b, 2019). Lapsarna has yielded rather indeterminate material, but still documents the presence of crocodylians and probably also lacertids, but differs from Kilçak in the presence of the urodelan *Mioproteus* (Vasileiadou et al., 2017). Kymi on the other hand has yielded only one herpetofaunal specimen, even though rather complete, i.e., the holotype (and only known specimen of the pythonid *Python euboicus* Römer, 1870). As such, Kymi is different from Kilçak, where the large snakes are so far totally unknown. Aliveri shares with Kilçak the presence of *Latonia*, Crocodylia, Lacertidae, *Ophisaurus*, and Colubridae, but differs in presence of *Chamaeleo* and Viperidae (Georgalis et al., 2016b, 2019). Karydia is also similar to Kilçak, sharing the presence of *Latonia*, lacertids, and anguids (Georgalis et al., 2019). Claessens (1997) reported remains of *Palaeobatrachus* sp. and *Bufo* aff. *viridis* from the early Miocene of Turkey, but we could not confirm this on the Kilçak material. Most probably, they occur here somewhat later, during the late early Miocene dispersal event (MN 3 – 4), when Asia Minor became connected to Europe. All taxa revealed in Kilçak are widely distributed in European faunas indicating that Anatolia had close faunal links to Europe during the late Oligocene-early Miocene. The snake fauna of Kilçak is remarkable by the presence of certain taxa documented from the area for the first time and therefore seems to be important by enhancing our knowledge in fossil record of several snake lineages, i.e. *Falseryx*, *Bavarioboa*, and *Texasophis*, whose record previously provided the earliest Miocene gap.

The fauna of Kilçak suggests the predominance of open habitats based on the presence of Lacertidae, *Ophisaurus*, and *Falseryx*. *Eoanilius* and *Texasophis* indicate a fossorial or semi-fossorial habitat (Ivanov and Böhme, 2011). *Latonia* prefers various types of aquatic or semiaquatic habitats. The occurrence of Crocodylia indicates the presence of lake and river systems (Georgalis et al., 2016c). But the dominance of heliophile forms over aquatic taxa suggests a relatively dry climate. Nevertheless, Kilçak palynoflora reflects a humid, warm-temperate climate (Yavuz and Demirer, 2018). The abundance of insectivores in Kilçak also supports the humid climate during the MN 1 (Van den Hoek Ostende, 2001c). The data of palynoflora and small mammals are compatible with the globally warm conditions maintained during the early Miocene. In contrast, the herpetofauna of the Kilçak generally corresponds to arid conditions similar to those of the late Oligocene. This contradiction can be partly explained by the existence of a mosaic of habitats ranging from steppe landscapes to freshwater lakes/rivers with surrounding vegetation, reflecting climatic fluctuations during the latest Oligocene to earliest Miocene transitional period.

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